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Effect of habitat quality on diet flexibility in Barbary macaques.

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Short title : overgrazing affects Barbary macaque diets

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ABSTRACT

Barbary macaques live in extreme temperate environments characterized by strongly seasonal resource availability. They are mainly terrestrial while foraging, harvesting food from the herbaceous layer. These monkeys are threatened mainly because of anthropogenic habitat degradation. We studied the adaptive capacities of wild groups of Barbary macaques that lived in different cedar forests undergoing varying extents of grazing pressure from domestic livestock. In all three sites, diet varied seasonally. Heavy grazing led to a significant decrease in herbaceous production and species richness. As a consequence, the monkeys' diet in this poor habitat showed a decreased plant species richness. Moreover, it incorporated fewer above-ground herbaceous resources, and a greater proportion of subterranean resources (especially hypogeous fungi and subterranean invertebrates such as earthworms, eggs and adults of earwigs, and ant's larvae) than the diet of monkeys inhabiting ungrazed forest. Cedar bark, cedar strobiles, earthworms and earwigs were part of the monkeys' diet only in grazed forest. Monkeys in heavily grazed forest compensated for a lack of herbaceous foods by eating subterranean foods preferentially to tree and shrub products. The foods they consumed take longer to harvest and process than the seeds or leaves consumed by Barbary macaques in less heavily grazed forest habitats. Our results suggest that monkeys do differ in their diets according to the degree of habitat change induced by human activities. They also highlight the dietary flexibility of Barbary macaques as a key element that allows them to cope with degraded habitats. We later compare the dietary adjustments of Barbary macaques facing environmental change to dietary strategies of other macaques and temperate-zone primates.
Key words : *Macaca sylvanus;* diet; habitat quality; grazing pressure; temperate forests.

INTRODUCTION

The expansion of human population results in spatial overlap between domestic livestock and wild animals, and competition will occur if they have to share food resources [Odadi et al., 2011]. Intense pastoralism may also lead to decreased habitat quality, which may endanger wild populations of herbivores [Bagchi et al., 2004; Bhattacharya & Sathyakumar, 2011; Sitters et al., 2009]. Generalist herbivores are more prone to persist in degraded habitats thanks to the great flexibility in their choice of food resources.

Acquiring food energy in conditions of food restriction (poor habitats or seasonal food shortage) involves the ability to change diet composition [Charnov, 1976; Di Fiore & Rodman, 2001; Emlen, 1966; MacArthur & Pianka, 1966; Schoener, 1971; Vasey, 2005]. Studies on non-human primates have shown that they may respond to a reduction in food availability by incorporating scarce but high-return foods or by optimizing their food intake on abundant but low-quality food [Hill et al., 2003; Sayers & Norconk, 2008; Tsuji et al., 2013; van Doorn et al., 2010; Wrangham et al., 1998]. The strategy they adopt may lead them to a diet including low profitability (e.g. energy/handling time) items (like Himalayan gray langurs, *Semnopithecus entellus,* in winter [Sayers et al., 2010]).

Most species of primates exhibit some degree of diet flexibility that allows them to cope with seasonality of resource availability or with inter-site differences of habitat quality due to altitude, latitude, habitat fragmentation/loss, or habitat degradation [Campbell-Smith et al., 2011; Chaves & Bicca-Marques, 2013; Chaves et al., 2012; Naughton-Treves et al., 1998; Quéméré et al., 2013; Riley, 2007; Singh et al., 2001; Tsuji et al., 2013; Xiang et al., 2007]. Even species broadly and stereotypically described as dietary specialists are able to modify their dietary composition in response to habitat change (folivores such as colobines, [Grueter et al., 2009b; Koenig & Borries, 2001; Sayers & Norconk, 2008; Sayers et al., 2010; Xiang et al., 2007], or frugivores [Russo et al., 2005; Wieczkowski & Kinnaird, 2008]). In addition, the

ability of monkeys to persist despite anthropogenic land transformation includes their ability to exploit resources from cultivated land or secondary habitats resulting from deforestation [Anderson et al., 2007; Campbell-Smith et al., 2011; Naughton-Treves et al., 1998; Quéméré et al., 2013].

Primate species living in temperate habitats should be considered amongst the most flexible primate because their habitats are characterized by marked seasonality of resource quality and abundance [Hanya et al., 2003; Hill, 1997; Hill & Dunbar, 2002; Tsuji & Takatsuki, 2009; van Schaik & Brockman, 2006]. In addition, seasonal variation in fruit production is higher in temperate forests than in tropical forests [Hanya et al., 2013], and fleshy fruit may be scarce for some temperate monkey species compared with tropical monkeys [Hanya & Aiba, 2010; Hanya et al., 2011; Ting et al., 2008].

Terrestrial or semi-terrestrial primate species, except the specialist graminivorous gelada baboons (*Theropithecus gelada,* [Dunbar & Bose, 1991], also have a highly omnivorous and flexible diet (several macaque species, [Goldstein & Richard, 1989; Hill, 1997; Zhao, 1996]; baboons, [Alberts & Altmann, 2006; Wahungu, 1998; Whiten et al., 1991; Whiten et al., 1987]). In addition, some of them extract a great amount of their resources from the herbaceous layer: as a result, they rank among the species most vulnerable to competition with domestic herbivores with domestic herbivores (e.g. [Sauther & Cuozzo, 2009]. Their diet flexibility is critical in allowing them to withstand habitat degradation and competition with domestic herds.

The Barbary macaque (*Macaca sylvanus)* is listed as "Endangered" on the Red List of Threatened Species, Appendix II of CITES [IUCN, 2013]. It is a terrestrial primate found primarily in extreme temperate regions, in mountain forests, similarly to Japanese macaques (*Macaca fuscata,* [Nakayama et al., 1999]), rhesus macaques (*M. mulatta,* [Qu et al., 1993]) and snub-nosed monkeys (*Rhinopithecus roxellana* and *R. bieti*, [Grueter et al., 2013; Su et

al., 1998]). Barbary macaque habitats are characterized by marked monthly variation in resource availability. In these habitats the snowy periods last several months, during which the available resources are mostly restricted to mature leaves of evergreen trees and lichens. A second period of food scarcity occurs during the summer months when herbaceous plants dry up [Ménard & Vallet, 1988; Ménard & Vallet, 1997]. Barbary macaques in different habitat types have a highly flexible diet. As months go by, they can shift from a mostly insectivorous diet to a granivorous, and finally a folivorous diet [Mehlman, 1988; Ménard, 1985; Ménard & Qarro, 1999; Ménard & Vallet, 1986].

Most wild Barbary macaque populations live in cedar-oak forests [Fa et al., 1984]. The largest population is located in the Middle Atlas in Morocco while other smaller populations are located in the cedar-oak forests of Algeria. The Middle Atlas forest presently suffers from heavy human pressure mainly due to overgrazing by sheep and goats [Lamb et al., 1991]. As Barbary macaques spend more than 50% of their mean annual feeding time on resources from the herbaceous layer [Ménard & Vallet, 1986], domestic herbivores such as sheep and goats that feed on the herbaceous plants are severe ecological competitors. Indeed, in forests where overgrazing was the highest, Barbary macaques increased their foraging and moving time, as well as daily travel distances (*i.e.* their energy costs), and spent less time feeding (*i.e.* ingesting food) than monkeys in less disturbed forests [Ménard et al., 2013]. Moreover, a recent study shows a negative correlation between livestock grazing intensity and monkey density, which suggests that monkeys could no longer find enough resources in forests where grazing pressure was high [Ménard et al., 2014].

In this paper, we describe the resource availability and diet of Barbary macaques living in three temperate cedar-oak forests undergoing varying intensities of livestock grazing. Because of the high seasonality of temperate habitats, we expected to find strong inter-month diet variation in all three forests. We expected that intense grazing by sheep and goats would

reduce the abundance and species richness of the herbaceous plants. As a corollary, we hypothesized that in the forest undergoing the most intense grazing pressure, monkeys would harvest their food more from the tree and shrub layers and/or use subterranean resources more than monkeys in the less heavily grazed forests. We also expected lower herbaceous plant species richness in their diet.

METHODS

Study sites, monkey groups and recording periods

The study sites were located in Algeria and Morocco. In Algeria, the Djurdjura National Park is located 4°8'E, 36°27'N, between 1100m and 1999m above sea level. It was created in 1983. In Morocco, the site of Aïn Kahla is located 5°12'W, 33°14'N and about 2000m above sea level, and the site of Seheb is located 5°14'W, 33°21'N, and 1500m above sea level. These two sites were located in the National Park of Ifrane, created in 2004 in the Middle Atlas. We studied one focal group *per* site. Group sizes ranged between 38 and 47 individuals in Djurdjura, 18 and 24 individuals at Aïn Kahla, and between 19 and 33 individuals at Seheb. Their home ranges were estimated to be 2.8 km² in Djurdjura [Ménard & Vallet, 1996], 1.8 km² at Aïn Kahla and 2.6 km² at Seheb [Ménard et al., unpublished data]. All home ranges mainly (> 70%) comprised mixed cedar-oak forests, oak forests, or cedar forests. Djurdjura site was composed of four vegetation types including 63% cedar-oak forest, 10% pure oak coppices, 24% open grassland, and 3% shrubby formation [Ménard & Vallet, 1988]. At Aïn Kahla and Seheb, we used a vegetation map from a study carried out in Ifrane park by a consulting agency whose information was checked before use [Sogreah-Ttoba, 2004]. According to that map, the two groups' home ranges (Aïn Kahla and Seheb) included more than 98% forests while open grasslands occupied less than 2%, and there were no pure oak coppices.

Livestock grazing was prohibited and almost absent in Djurdjura, intermediate at Aïn Kahla, and intense at Seheb. At each site, an estimate of the grazing pressure was available for each "parcel" referenced by foresters and was drawn from Sogreah-Ttoba reports [Sogreah-Ttoba, 2004]. A "parcel" is a delimited area subjected to a uniform management program by forestry managers. Each parcel, including those in the home ranges of our groups, was characterized by an index ranging from 0 (minimum pressure: < 2 small ruminants (sm)/ha/day) to 2 (intense pressure: > 5 sm/ha/day). Observers verified this classification during the years of the study (2006-2008).

We carried out observations in Djurdjura between April 1983 and March 1985 (seven months, September to January excluded), at Ain Kahla between July 2006 and August 2008 (13 months, September-January excluded) and at Seheb between April 2007 and August 2008 (11 months, September-January excluded). Livestock entered the forest to graze from February to August, *i.e.* during the winter (February-March), spring (April-June) and summer (July-August) seasons.

Data collection

We estimated visually the percentage of cover (0-10%; 11-25%; 26-50%; 51-75%; > 75%) of each tree and shrub species (*i.e.*. their abundance) in 25-m radius plots located at the corners of 50m x 50m grid cells covering a broad proportion of the groups' home ranges (580 plots in Djurdjura, 291 at Aïn Kahla and 432 at Seheb). Their overall surface represented 32-40% of the home range areas. We used the median values of the cover classes to calculate the mean percentage cover of each species at the three sites.

We studied herbaceous species richness in spring at the peak of vegetation growth, and monthly variation in herbaceous abundance from February to August in the three sites. These measurements were carried out in 2008 at Aïn Kahla and Seheb and were drawn from a study conducted in 1984 in Djurdjura [Ménard & Vallet, 1988; Ménard & Vallet, 1996]. We

estimated species richness in 1m x 1m quadrats (47 in Djurdjura, 7 each at Aïn Kahla and Seheb) placed at the intersection of a 200-m grid covering the group's home range in Djurdjura, and every 200m along a 1.2-km transect in each home range of the Aïn Kahla and Seheb groups. We sampled fewer quadrats at Aïn Kahla and Seheb than at Djurdjura owing to lower diversity of vegetation types in the groups' home ranges (see above). In each quadrat, we recorded the presence/absence of each species. In addition, we recorded more occasional species (not found during quadrat sampling) *ad libitum* when observers moved around in the field. During monthly replicates, we measured global herb cover (%) as an indicator of monthly and inter-site variation in herbaceous abundance. In Djurdjura, monthly replicates were limited to 23 of the 47 quadrats due to schedule constraints related to behavioral observations. In doing so, however, we lost little in relative precision (defined as the ratio of the half-size of the confidence interval at alpha=0.05, 2.08% of the estimate of the herbaceous cover), which ensured a good approximation of the herb cover while dividing the sampling effort by two.

We conducted behavioral observations from dawn to dusk, and equalized observation times across the daylight hours. We recorded a total of 477, 890 and 750 hours of observations from the Djurdjura, Aïn Kahla and Seheb groups, respectively. Visibility was good at all sites, and animals were habituated to observers, who typically approached them as close as 3-10m. We collected diet data (plant names and parts eaten) by scan sampling, at 15-min intervals [Altmann, 1974], of five individuals observed from a right to left direction to avoid food item bias. We recorded food items at each feeding occurrence, *i.e.* the picking and ingestion of food items (foraging excluded). We categorized individuals as follows: adult males and females, more than 5 years old; sub-adult individuals, 3 and 4 years old; juveniles, 1 and 2 years old. To obtain as complete a record as possible of diet composition, we also

recorded *ad libitum* rarely eaten food species that were not observed during the scan sampling procedure. These qualitative observations were not included in the statistical analysis.

Data analyses and statistics

The herbaceous plant sampling effort varied between the three sites. Because the observed number of species depends on sample size, our estimations of herbaceous species richness were standardized for comparisons. We produced sample-based rarefaction curves, which are plots of randomized richness *vs.* sampling effort, *i.e.* the number of quadrats [Gotelli & Colwell, 2001]. Rarefaction generated the expected number of herbaceous species in sets of *n* sampled quadrats as well as the 95% confidence intervals. We used Mao Tau randomizations computed with EstimateS [Colwell et al., 2004]. We then compared average species richness *per* sampling unit over the three sites using randomization tests. Computations required Monte Carlo re-sampling [Manly, 1997], so we used the *rich* package (function *c2m*) in R [Rossi, 2011]. We also approximated the "true species richness" computing Chao2 estimators with EstimateS [Colwell, 2011].

We used Generalized Linear Models (*GLMs*) and analysis of deviance (*anova* function in R [R Development Core Team, 2010]) to test for the effects of month and site on the percentages of herb cover (*i.e.* the monthly means of the sampled quadrats). We analyzed all subsets of models containing the 'month' and/or 'site' predictors (Table 1). *GLMs* used binomial errors for proportion data and a logit-link function [McCullagh & Nelder, 1989]. We based model selection on Akaike's information criterion corrected for small samples (AICc, [Burnham & Anderson, 2002]). We chose the model with the lowest AICc as the best fitting and the most parsimonious one. We calculated the Akaike weight (w_i) for each model, which can be interpreted as the probability for model *i* to be the best model to explain the observed variation in plant cover. Models with an AICc difference below 2 (ΔAICc <2) have substantial support and should be considered [Burnham & Anderson, 2002]. Variable importance was

estimated by summing the Akaike weights across models containing each predictor variable [Burnham & Anderson, 2004]. We used MuMIn package in R (function *model.avg*) for these calculations.

We expressed the composition of monthly diets as the percentage of time spent feeding on food species (Appendix A) and on 10 food categories (above-ground herbaceous resources, cedar seedlings, leaves and flowers of trees and shrubs, shrub fruit, acorns, roots, mushrooms, subterranean invertebrates, cedar bark, lichens). Subterranean invertebrates are ant's larvae, adults or eggs of earwigs, or earthworms. Cedar bark is the inner cambium and phloem through which the sap flows. Owing to diverging diets depending on Barbary macaques' age and sex classes [Ménard & Vallet, 1997], we calculated mean monthly diet as the average of the mean diet of the four age/sex categories (adult male, adult female, subadult individual, juvenile individual). We pooled observations from the same month across the years. We calculated a mean diet for the study period by averaging the monthly values for each food category.

We produced sample-based rarefaction curves and computed Chao2 estimators to compare herbaceous species richness to the "true species richness" of the diets [Colwell, 2011]. Rarefaction generated the expected number of species eaten in sets of *n* sampled hours that included feeding occurrences. We then plotted the randomized number of species as a function of the number of eaten food items as computed with EstimateS. We tested diet richness differences between sites using function *c2m* (*rich* package, [R Development Core Team, 2010; Rossi, 2011]).

We used MANOVA with Roy test to investigate the effect of month, site, and the additive effect of 'month and site' on the percentage of time spent feeding on the 10 food categories [R Development Core Team, 2010]. We transformed our data, which consisted of proportions, using the arcsine square root. This transformation normalized the proportions.

Our research was consistent with the Principles for the Ethical Treatment of Non Human Primates of the American Society of Primatologists. Data collection was based on non-invasive behavioral observations. All investigations reported in this manuscript comply with the current law in Morocco and Algeria and were conducted in close partnership with Moroccan Forestry authorities and the managers of the Djurdjura National Park in Algeria.

RESULTS

Vegetation characteristics and resource availability

At all three sites, the tree layer was dominated by cedars (*Cedrus atlantica,* 50% cover in Djurdjura, 57% at Aïn Kahla, 66% at Seheb) while holm oak (*Quercus rotundifolia)* was the second most common species (23% in Djurdjura, 53% at Aïn Kahla, 21% at Seheb). Other species (*Pinus clusiana, P. halepensis, Populus nigra* in Djurdjura; *Acer monspessulanum, Sorbus torminalis* at Aïn Kahla and Seheb) occupied less than 7% of the tree cover.

Global shrub cover in the monkeys' home ranges was greater in the Moroccan forests (44% at Aïn Kahla and 45% at Seheb) than in Djurdjura (14%). However, species richness was highest in Djurdjura (26 species), intermediate at Aïn Kahla (11 species) and lowest at Seheb (8 species). Only six species were common to the three sites.

None of the rarefaction curves (Fig. 1) reached true herbaceous species richness. Estimated species richness (using Chao2 estimator) was 203 species in Djurdjura, 99 at Aïn Kahla and 33 at Seheb. When we added the species observed *ad libitum*, variation among sites remained similar (240, 107 and 41 species, respectively). Comparing species richness based on a standardized number of quadrats (N = 7), we found significantly higher richness values in Djurdjura than in Seheb, and in Aïn Kahla than in Seheb (Monte Carlo randomization test: $P < 0.01$), while we failed to detect a significant difference between Djurdjura and Aïn Kahla ($P = 0.39$).

The model that best explained variation in herbaceous plant cover included month, site and the interaction between month and site (Table 1). The sum of all Akaike weights showed 'month' and 'site' as equally important predictors (Sum*(w*AICc) = 1.00, Table 1). Monthly variation was significant ($\chi^2 = 1424.97$, df=6 , $P < 0.001$) but differed significantly among sites, with plant cover reaching a peak in April at Aïn Kahla and Seheb and in May in Djurdjura ($\chi^2 = 604.34$, df = 12, $P < 0.001$; Fig. 2). Plant cover varied significantly across sites ($\chi^2 = 285.39$, df = 2, $P < 0.001$) : it was lower at Seheb than at the two other sites and lower in Djurdjura than at Aïn Kahla (Table 1).

Diet composition

We made a total of 2027, 4654 and 3205 feeding records from the Djurdjura, Aïn Kahla and Seheb groups, respectively. At all three sites, tree products in the monkeys' diets mainly came from the two dominant species, *i.e. Cedrus atlantica* and *Quercus ilex*. At Seheb and Aïn Kahla, Barbary macaques consumed barely half as many shrub species as compared to Djurdjura macaques (see details in appendix A). Comparing herbaceous species richness at a standardized number of hours of recordings (N = 191) we found a significantly richer diet in Djurdjura *vs.* the two other sites and in Aïn Kahla *vs.* Seheb (Fig. 3, Monte Carlo randomization tests: $P < 0.01$, see also details in appendix A). Estimated species richness (using Chao2 estimator) was 65 species in Djurdjura, 49 at Aïn Kahla and 31 at Seheb. In Djurdjura, this value approximates the true diet richness (74 herbaceous plant species, see also appendix A) obtained when rarely eaten species, observed *ad libitum,* were included.

In each site, more than 79% of the herbaceous species of the diet were recorded in the quadrats. Each of the remaining species composed less than 0.05% of the monthly diet. Thus the sampled quadrats reflected quite well the herbaceous species available for monkeys in their respective habitats.

Diets varied significantly by month and by site (Fig. 4). The model with the lowest AICc included 'month + site' (MANOVA, month : $F_{6,12}$= 24.03, P < 0.001; site : $F_{2,12}$= 13.39, P < 0.001).

Variation in the monkeys' diet was explained by strong monthly changes in the proportions of almost all food categories (Fig. 4, Table 2). During winter months and in early spring (from February to April), the staple foods were above-ground herbaceous resources and/or cedar seedlings at all three sites (Fig. 4). In the following months (from May to August) monkeys consumed an increasing proportion of different subterranean resources (roots, mushrooms, invertebrates), shrub fruit, and/or acorns (Fig. 4). Consumption of cedar bark peaked at 18% in May at Aïn Kahla and 21% in June at Seheb.

Monkeys' diets in Djurdjura and at Aïn Kahla relied significantly more on the above-ground herbaceous resources (58.3% and 47.6% on average, respectively) than at Seheb (22.3%, Fig. 4, Table 2). By contrast, among the subterranean resources, Seheb monkeys ate significantly more mushrooms (13.3% on average) and invertebrates (ant larvae, adults or eggs of earwigs, or earthworms; 6.9%), than monkeys at the two other sites (mushrooms < 3%; invertebrates < 1%). In parallel, they consumed significantly less roots (4.6% on average) than in Djurdjura (9.7%, Fig. 4, Table 2). This inter-site variation in the consumption of the different subterranean resources categories and of above-ground herbaceous resources was especially marked in late spring and summer (June to August, Fig. 4). The contribution of the tree and shrub resources (leaves and flowers, acorns, cedar seedlings, fruit) and lichens in the diets did not differ significantly between the three sites (Table 2). Although cedar bark was eaten only at Aïn Kahla and Seheb, our results only suggest a tendency toward differential cedar bark consumption between these two sites and Djurdjura (P = 0.08, Table 2, Fig. 4), possibly because of a lack of statistical power. Consumption of cedar male flowers also varied among sites, although it was not a major food class. It contributed to the monkeys' diet at Aïn

Kahla and Seheb (up to 12% in August) while it was never observed in the diet of Djurdjura monkeys (Appendix A). Lichens were also a minor food item (~ 1.5% of the diet on average), but did contribute at all three sites.

DISCUSSION

Influence of human pressure and seasonality on habitat quality

In the Moroccan forests where grazing was intense (Seheb), plant species richness, especially herbaceous plant richness, was lower than in the other less intensively grazed forests of Djurdjura and Aïn Kahla. The high species richness in Djurdjura reflects a greater variety of vegetation types as well as the absence of grazing pressure. The abundance of herbaceous plants, in terms of herb cover, was also lowest in the forest undergoing the most intense grazing pressure (Fig. 2). Differences in species richness and abundance at the herbaceous layer level were already apparent when vegetation sprouted in February-March, before grazing started. Because of its long-term effects on vegetation [Chaideftou et al., 2009], intense grazing pressure is probably the main factor that accounts for these differences between sites, in particular between Aïn Kahla and Seheb where forest formations were relatively comparable among the groups' home ranges. Indeed, overgrazing severely and durably reduced herb species richness and abundance in other Mediterranean forests [Chaideftou et al., 2009]. Based on grazing intensity, we did not expect overall greater abundance of herbaceous plants at Aïn Kahla *vs.* Djurdjura. This difference may reflect climate differences. Snow persisted until March in Djurdjura, and herbaceous growth started two months later than at Aïn Kahla and Seheb. In addition, the plant cover dried earlier in Djurdjura (Fig. 2).

Seasonal dietary flexibility – importance of subterranean resources

Seasonal dietary flexibility has been described in many primate species in tropical as well as in temperate regions (see review in [Hemingway & Bynum, 2005]). Like other

monkeys living in temperate habitats (*e.g.* [Grueter et al., 2009b; Guo et al., 2007; Hanya et al., 2003; Hill, 1997; Tsuji et al., 2006; van Doorn et al., 2010]), the macaques we studied showed marked monthly variation in their diet. It consisted of rapid adjustments to abrupt changes in food availability that characterize extreme temperate environments where most productions (budding, flowering, fruiting, and seed production) are highly synchronized. Our results are in line with studies of Barbary macaques in other habitat types (deciduous oak forest, [Ménard, 1985]; fir forest [Mehlman, 1988]), which suggest general patterns of seasonal dietary changes for the species. In particular, Barbary macaques use a large amount of subterranean resources in the dry months of food scarcity (up to > 56% in cedar-oak forest, this study, Fig. 4; up to > 34% in deciduous oak forest, [Ménard, 1985], common in fir forest, [Mehlman, 1988]). This diet shift also occurs in other temperate/terrestrial species such as savannah baboons (up to 53% of the diet, [Alberts et al., 2005; Whiten et al., 1991]), and to a lesser extent Himalayan gray langurs (up to 13% [Sayers & Norconk, 2008]), and snub-nosed monkeys (low quantities, [Grueter et al., 2009b]). By contrast, this shift is less common in tropical primates : underground resources represent very low quantities in their diet, even in tropical forest baboons' diet [Kunz & Linsenmair, 2007]. Although other temperate macaques share similar patterns of diet seasonality with Barbary macaques, to our knowledge few of them rely on underground resources (see a review in [Ménard, 2004]), except, to a lesser extent, *Macaca mulatta* (23.7% in winter, [Goldstein & Richard, 1989]), *M. fuscata* (< 3% during the dry winter season, [Hanya, 2004]), and *M. munzala* (6.7% of winter food includes roots, tubers, stems and sepals taken together [Mendiratta et al., 2009]). Therefore, some diet characteristics of *M. sylvanus* appear closer to savannah baboons' than to most other macaque species'.

Influence of habitat quality on diet

As a consequence of differences in habitat quality between the sites, the specific richness of the monkeys' diet was lower in the forest undergoing most grazing (Seheb). Lower diet diversity was also observed in *Rhinopithecus bieti* [Xiang et al., 2007] and in *M. tonkeana* [Riley, 2007] in poor habitats whereas anthropogenic landscape alteration did not influence diet richness of golden-crowned sifakas (*Propithecus tattersalli)* thanks to their ability to utilize both forest fragments and matrix habitats [Quéméré et al., 2013]. Therefore, the way habitat quality affects diet richness may depend on monkeys' ability to adapt to new habitats or to exploit new compartments of their environment.

Our results suggest that Barbary macaques prefer above-ground herbaceous resources, when available, rather than arboreal or shrub resources (*e.g.* cedar leaves that were abundant in all study sites). Indeed, in the site least affected by livestock, where cedars (and likely cedar foods) were as available as in the overgrazed forest, monkeys preferred to eat herbaceous plants, and they consumed them two times more (>48% on average) than in overgrazed forest (22%, Fig. 3). Therefore, herbaceous plants appear as a limiting resource.

In the site where grazing pressure was high and above-ground herbaceous resources were scarce, monkeys' diets included more subterranean than above-ground herbaceous foods (25% *vs.* 22% on average, Fig. 4, Table 2). In addition, they compensated for the reduced above-ground herbaceous resources by preferentially exploiting the subterranean layer rather than shifting to arboreal and shrub resources. Therefore, these results suggest that monkeys adjusted their diet according to the availability of herbaceous resources. In the least grazed sites, monkeys devoted five times less time to feeding on subterranean resources than on above-ground plants.

In the two grazed forests of the Middle Atlas (Aïn Kahla and Seheb), we noticed the consumption of cedar bark, cedar strobiles, earthworms and earwigs. This had never been observed in the preserved cedar-oak forest of Djurdjura (Appendix A, [Ménard & Vallet,

1988]; Ménard and Vallet, unpublished data from behavioral studies conducted between 1985 and 1993). Earthworms and earwigs were also unknown monkeys' invertebrate preys in the deciduous oak forest of Akfadou in Algeria where livestock were almost absent ([Ménard, 1985]; Ménard and Vallet, unpublished data from behavioral studies conducted between 1985 and 1992). By contrast, previous studies mentioned the presence of cedar bark, cedar strobiles and earthworms in monkey's diet in cedar forests of the Middle Atlas [Deag, 1983; Drucker, 1984] and in a fir forest of the Rif in northern Morocco [Mehlman, 1988] that underwent heavy grazing by livestock. It appears that Barbary macaques fed on a separate niche from domestic herbivore competitors in the herbaceous layer in grazed forests. This implies innovative ways of acquiring alternative foods, from the underground or arboreal layer (*e.g.* extractive foraging for subterranean invertebrates or sucking cedar strobiles to ingest the resin before rejecting them). Interestingly, Mehlman [1988] describes another innovative feeding technique in the fir forest of the Rif, *i.e.* "tadpole fishing" in the shallow pools of the streams. These findings highlight dietary flexibility as a key element for Barbary macaques to cope with changing environments.

In all three sites, acorns were an extensive component of the diet in August. Ménard and Vallet showed that acorns can constitute a staple food at least for four months and can be eaten from July (unripe acorns) to March (fallen acorns found under fallen leaves or snow) in evergreen cedar-oak or in deciduous oak forests [Ménard, 1985; Ménard & Vallet, 1986]. Similar patterns were observed in a fir forest [Mehlman, 1988]. These highly energetic food items, rich in soluble carbohydrates and fat, although not in protein [Abbas et al., 2011], enable monkeys to replenish their energy reserves before the winter months. Species of the genus *Quercus* or related genuses of the Fagaceae family (*Cyclobalanopsis, Lithocarpus)* provide comparable lasting key resources to other temperate primates (*R. bieti,* [Grueter et al.,

2009a; Xiang et al., 2007]; *R. roxellana,* [Guo et al., 2007]; *M. thibetana,* [Zhao et al., 1991]; *M. fuscata,* [Agetsuma & Nakagawa, 1998; Hill, 1997]).

Did Barbary macaques rely on fallback foods?

Many species of primates overcome periods of food scarcity by relying on fallback foods when preferred items are unavailable (*e.g.* [Marshall & Wrangham, 2007]; grass corms during a dry summer, [Altmann, 2009]; bark, lichens, invertebrates, or leaves during dry winters [Grueter et al., 2009b]).

Bark is included in the diet of many primate species to varying extents in tropical [Chaves & Bicca-Marques, 2013; Cristobal-Azkarate & Arroyo-Rodriguez, 2007] and temperate habitats [Grueter et al., 2009b; Guo et al., 2007; Hanya, 2004; Xiang et al., 2007; Zhao et al., 1991]. It appears as the most common fallback food for temperate primates in winter [Grueter et al., 2009b] and is also considered as an adaptation to extreme habitats in *Rhinopothecus bieti* [Xiang et al., 2007].

In Barbary macaques, bark stripping occurred between May and August, and reached a maximum of about 20% of their feeding time. We observed a relatively high level of bark stripping even when herbaceous resources were plentiful, confirming previous findings from a preliminary study conducted in 1995 at Aïn Kahla [Ménard & Qarro, 1999]. These findings suggest that bark is not a fallback food for Barbary macaques.

It takes a long time to process cedar bark compared to foods like herbaceous leaves or seeds (mean number of consumption units of a food *per* minute spent foraging and feeding: about six for bark *vs.* up to 48 for leaves and 33 for seeds; Ménard et al., unpublished data). The consumption of bark, despite the long handling time and the availability of other resources, suggests that cedar sap may provide important nutrients unavailable in other foods. Tree exudates consumed by various Callitrichidae or patas monkeys (*Erythrocebus patas)* are rich in calcium and can counter-balance a diet that is poor in that mineral [Garber, 1984;

Isbell et al., 2013; Smith, 2000]. Grazing pressure, which induces lower species richness in forests, can lead to a monotonous diet unlikely to span the whole range of the monkeys' nutritional needs. However, we need further analyses on the nutritional quality of bark and other food items to confirm this hypothesis. The increased bark stripping by monkeys noticed by foresters in the Middle Atlas over the last 20 years [Et-Tobi et al., 2009] may result from a grazing-induced decrease in herbaceous species diversity.

Lichens have been observed in the diet of other temperate monkeys as fallback foods during periods of food scarcity [Grueter et al., 2009b; Kirkpatrick & Grueter, 2010]. In Barbary macaques living in a deciduous oak forest, lichens composed up to 43% of the monthly diet in winter and 17% in summer, when preferred foods are relatively scarce [Ménard, 1985]. In this site, lichens could be fallback foods. At Aïn Kahla and Seheb, the limited consumption of lichens (< 3.2%) during periods of food shortage could reflect a low availability of this resource which is extensively harvested by local people for traditional medicine [Bellakhdar et al., 1991].

Conclusions and perspectives regarding Barbary macaque foraging strategy

This study provides evidence of dietary flexibility in Barbary macaques. They survive in altered habitats by exploiting alternative food resources (*e.g.* subterranean foods or cedar bark) that escape from their main competitors, *i.e.* sheep and goats. At the same time, they avoid food items that are available year-round such as cedar leaves. However, by foraging on scarce, difficult-to-excavate foods, monkeys increase their energy costs by spending more time foraging and moving, and increasing group's day range lengths [Ménard et al., 2013]. Our findings suggest that Barbary macaques adopt an energy-maximizing strategy in the summer period of food scarcity, confirming previous studies performed during a comparable time of year [Ménard & Vallet, 1997]. Further studies on food handling time, daily dry weight intake and energy intake would be useful to assess the profitability of foods (energy/handling

time, [Sayers et al., 2010]), and to specify whether Barbary macaques' foraging strategies lead them to incorporate scarce but high-return foods in their diet. These developments would bring new, valuable knowledge for the preservation of the species.

Overgrazing, through its negative effects on habitat quality, depresses population density [Ménard et al., 2014]. These findings suggest that, despite their dietary flexibility, monkeys may not cope fully with anthropogenic changes in their habitat. High levels of foraging effort may induce considerable energetic stress that affect female reproductive strategies [Foerster et al., 2012], especially by preventing successful lactation, and in turn inducing lower infant survival.

Maintaining sustainable populations of Barbary macaques in the Middle Atlas requires urgent changes in the management of forests, especially by reducing the number of grazing sheep and goats. Additionally, we recommend allowing holm oaks to fully develop in the Middle Atlas instead of using clear-cutting sylvicultural pratices in order to preserve the production of acorns, a crucial food resource for Barbary macaques before the stress of the winter season.

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FIGURE LEGENDS

Figure 1: Herbaceous species richness in the three sites. Rarefaction curves represent the cumulative number of recorded species, *i.e.* randomized species richness, as a function of the number of sampled quadrats. Dashed lines delineate 95% confidence intervals.

Figure 2: Monthly variation in herb cover (%) in the three sites. Bars represent standard deviations.

Winter: February-March; Spring: April-June; Summer: July-August.

Figure 3: Herbaceous species richness in the monkeys' diets at the three sites. Rarefaction curves represent the cumulative numbers of recorded species. Randomized species richness is represented as a function of the number of feeding records. Dashed lines delineate 95% confidence intervals.

Figure 4. Variation in the percentage of feeding time spent on 10 food categories depending on month and site.

Winter: February-March; Spring: April-June; Summer: July-August.

Table I. Comparisons of models of herb cover as a function of month and site, showing model selection statistics and results for inter-site comparisons.

Subsets of models	k	Deviance	AICc	ΔAICc	*wi*	Sum(*w*AICc)	Estimate	*SE*	*z*	P
Month * site [a]	21	1870.8	2767.3	0.00	1.0					
Month + site	9	2475.1	3343.9	576.6	0.0					
Month	7	2760.5	3625.0	857.7	0.0	**1.0**				
Site	3	3900.1	4756.2	1988.9	0.0	**1.0**				
Djurdjura – Aïn Kahla							0.52	0.08	6.48	<0.001
Djurdjura – Seheb							-0.85	0.12	-6.97	<0.001
Aïn Kahla - Seheb							-1.37	0.13	-10.59	<0.001

AICc, Akaike's information criterion corrected for small sample sizes; *wi,* Akaike's information criterion weights for each model; Sum*(w*AICc), the relative importance of predictor variables was assessed by summing the Akaike weights from each model containing that predictor. The highest values are in bold-type.

[a]: Month x site stands for month + site + month:site (effect of month, plus effect of site plus effect of the interaction of month and site). See text for calculation details.

Table II. Statistical analyses of the monthly and inter-site variations of monkey diets. Results of the MANOVA analyses of the additive model "month + site".

Food items	$F_{8,12}$	R^2_{adj}	P value	Inter-site	Estimate[a]	SE	*t*	P value
Cedar bark	2.46	0.37	0.08					
Cedar seedlings	5.60	0.65	**< 0.01**					
Tree and shrub leaves and flowers	0.63	- 0.17	0.74					
Shrub fruits	2.34	0.35	0.09					
Above-ground herbaceous resources	7.37	0.72	**<0.001**	Aïn Kahla-Seheb	-0.29	0.08	-3.60	**<0.01**
				Djurdjura-Seheb	-0.41	0.08	-5.01	**<0.001**
Acorns	3.23	0.47	**<0.05**					
Roots	6.52	0.69	**<0.01**	Djurdjura-Seheb	-0.14	0.05	-2.53	**<0.05**
Invertebrates	4.20	0.56	**<0.05**	Aïn Kahla-Seheb	0.12	0.05	2.54	**<0.05**
				Djurdjura-Seheb	0.20	0.05	4.01	**<0.01**
Mushrooms	3.89	0.54	**<0.05**	Djurdjura-Seheb	0.30	0.07	4.53	**<0.001**
				Aïn Kahla-Seheb	0.20	0.07	2.97	**<0.05**
Lichens	0.46	- 0.27	0.86					

Significant variations are given in bold.

[a] When the variations involved significant difference between sites, the decomposition of the P value is specified.

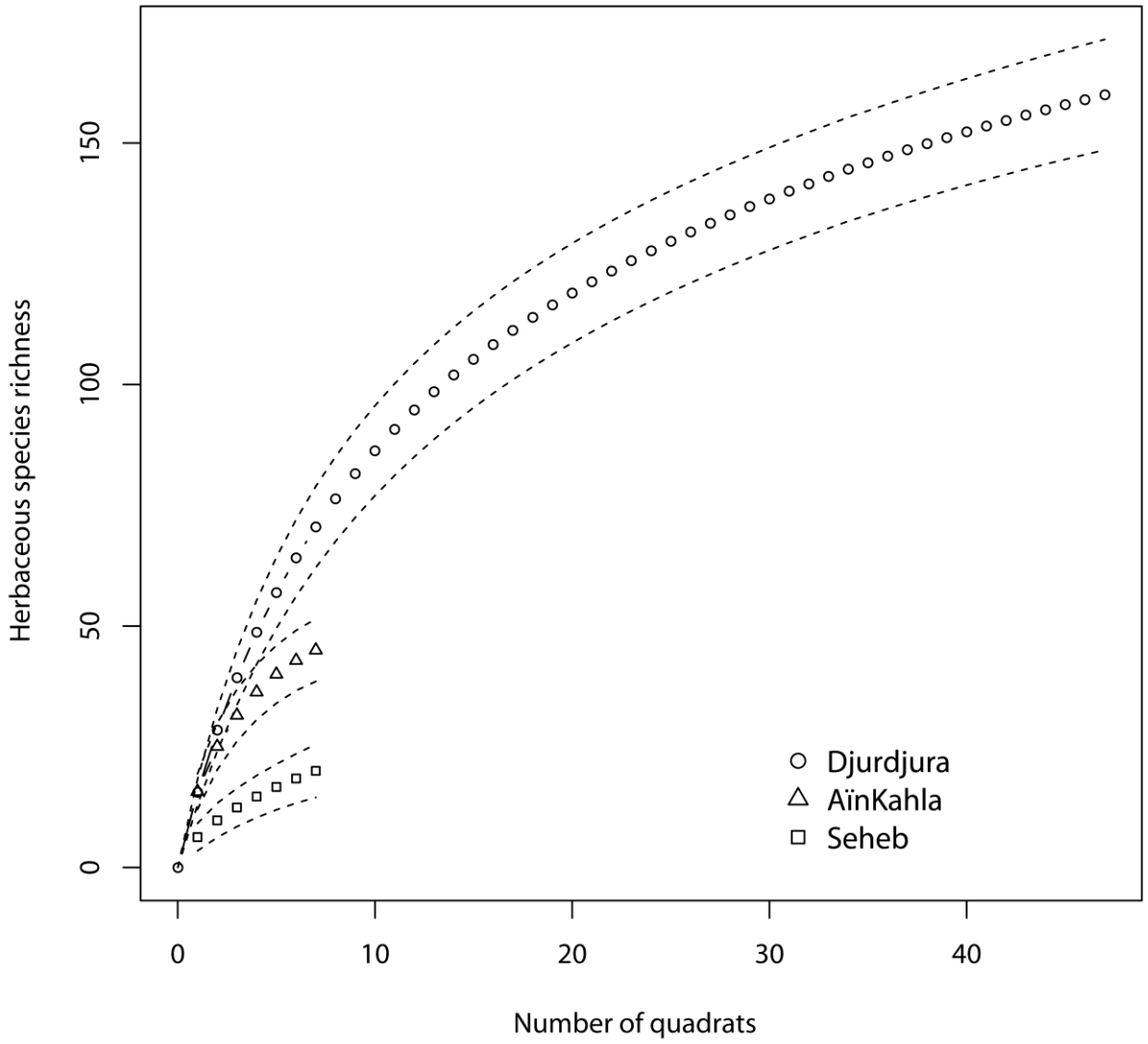
Herbaceous species richness
0
50
100
150
0
10
20
30
40
Number of quadrats
Djurdjura
AïnKahla
Seheb

Fig.1

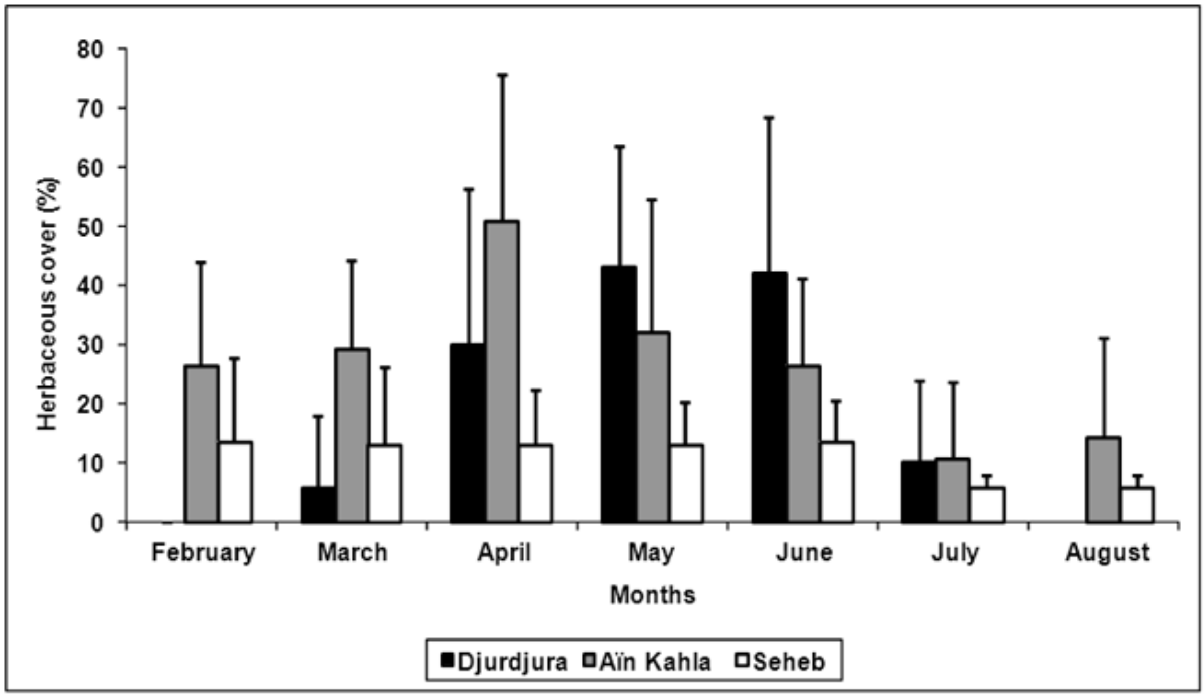
Herbaceous cover (%)
80
70
60
50
40
30
20
10
0
February
March
April
May
June
July
August
Months
Djurdjura
Aïn Kahla
Seheb

Fig.2

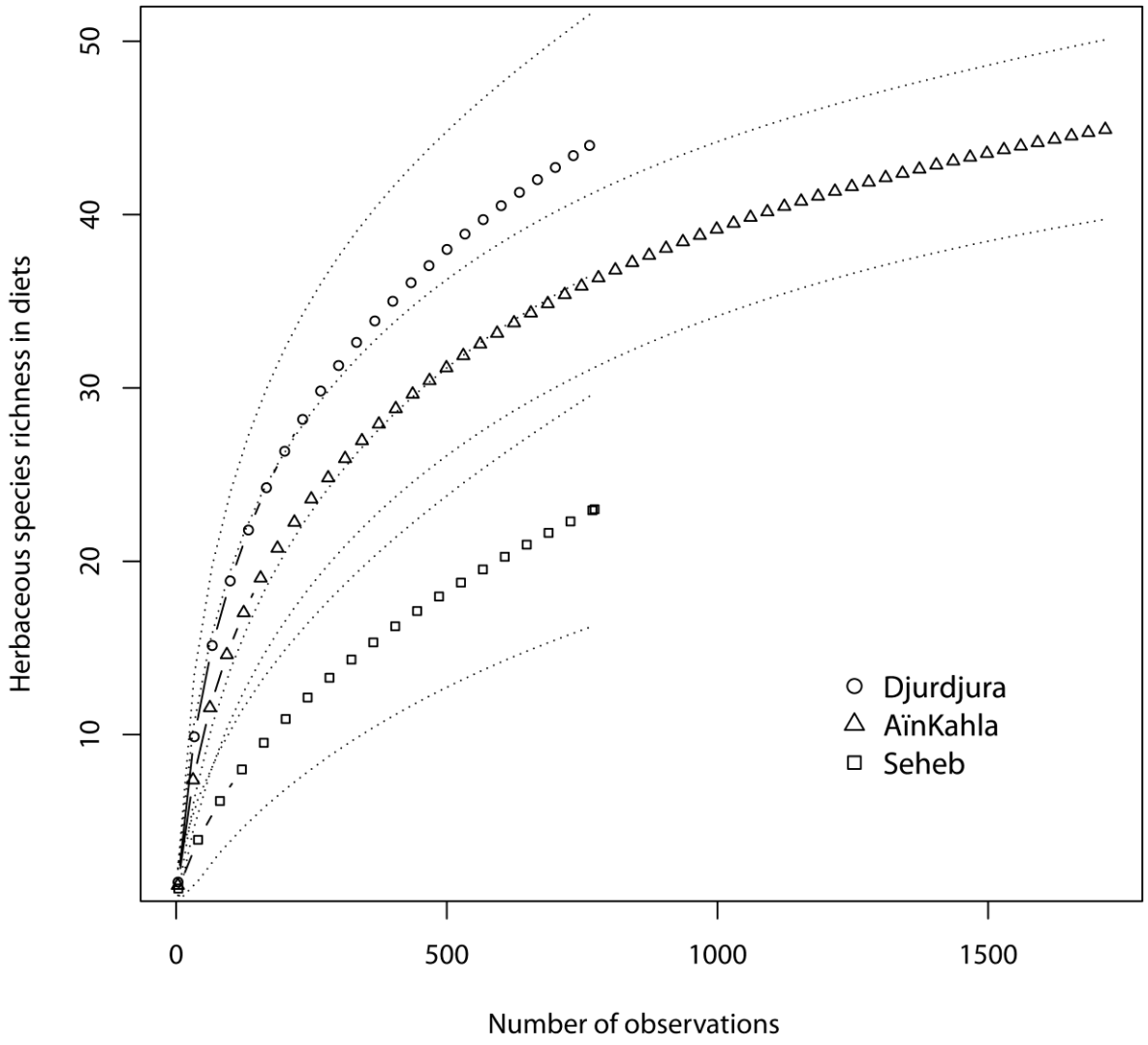
Herbaceous species richness in diets
10
20
30
40
50
0
500
1000
1500
Number of observations
Djurdjura
AïnKahla
Seheb

Fig.3

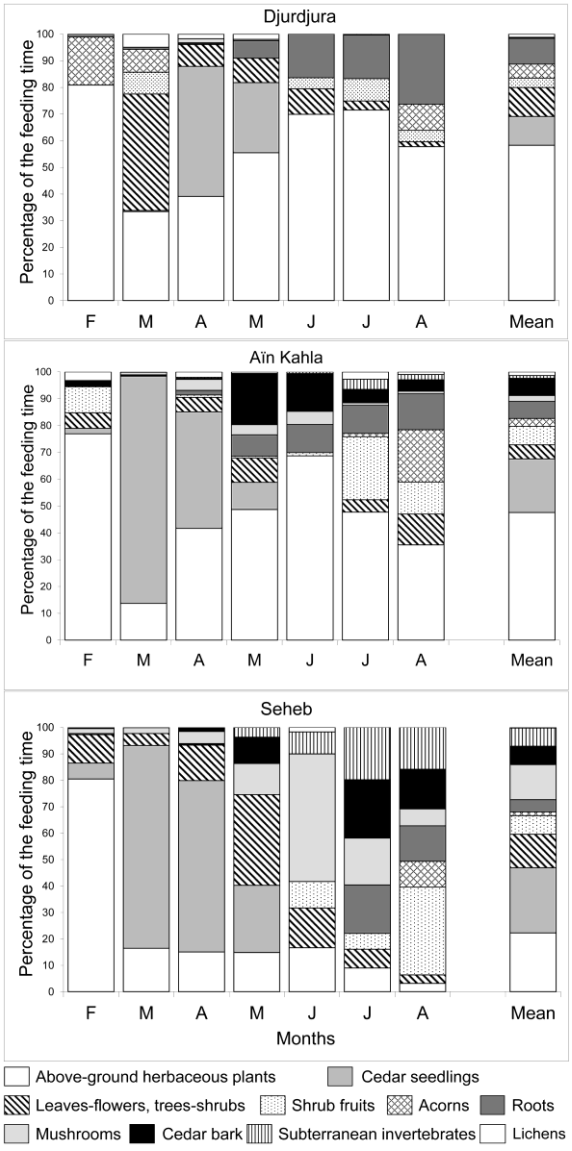
Djurdjura
Aïn Kahla
Seheb
Percentage of the feeding time
F M A M J J A Mean
Months
Above-ground herbaceous plants
Cedar seedlings
Leaves-flowers, trees-shrubs
Shrub fruits
Acorns
Roots
Mushrooms
Cedar bark
Subterranean invertebrates
Lichens

Fig.4

Appendix A. Specific composition of the Barbary macaque diet (as average of monthly percentages of feeding time) and monthly occurrences (x) at the three sites. For each species, the highest monthly percentage is given in parentheses and the associated month is indicated in bold.

Sites		Djurdjura	Months							Aïn Kahla	Months							Seheb	Months						
Species	Part(s) eaten	% eating	F	M	A	M	J	J	A	% eating	F	M	A	M	J	J	A	% eating	F	M	A	M	J	J	A
Tree layer																									
Cedrus atlantica	L,Sg	4.9 (33.1)		x	**x**	x				23.2 (84.9)	x	**x**	x	x		x	x	30.0 (79.1)	x	**x**	x	x		x	x
	Ms									2.0 (12.4)						x	**x**	+ (0.3)							**x**
	B									6.4 (17.2)	x		x	**x**	x	x	x	6.1 (23.2)	x		x	x		**x**	x
Pinus clusiana	Fl	0.2 (1.6)		**x**																					
Populus nigra	L,Fl	1.4 (7.4)		x	**x**																				
Quercus ilex	L,Fl	1.2 (4.1)		x		x	**x**											0.2 (1.1)				**x**			
	Ac	5.2 (18.0)	**x**	x	x				x	2.7 (18.1)						x	**x**	1.5 (10.2)							**x**
Acer monspessulanum	L									0.5 (2.8)			**x**	x		x		+			**x**				
Sorbus torminalis	L																	+				**x**			
Lichens		1.2 (4.9)		**x**	x	x				1.2 (3.2)	**x**		x	x		x	x	0.3 (1.7)			x		**x**		
Shrub layer																									
Taxus baccata	F									1.4 (9.7)	**x**	x					x								
Juniperus oxycedrus	F	1.0 (5.1)		x				**x**	x																
Juniperus communis	F	+						**x**																	
Juniperus thurifera	L,F									0.8 (2.5)	x		x				**x**								
Berberis hispanica	L	0.3 (1.8)							**x**																
Ribes grossularis	L,F									4.2 (20)	x		x	x	x	x	**x**	1.8 (3.3)	x	x	x	x	**x**		x
Rosa sp.	L,F,St	1.7 (11.1)		**x**					x	1.1 (3.5)					x	x	**x**	4.8 (14.9)		x	x	x	x	x	**x**
Rubus sp.	L,F,St									+							**x**	3.4 (15.3)					x		**x**
Crataegus laciniata	L,Fl,F	0.4 (2.7)					**x**			0.3 (2.0)			x	**x**				6.2 (25.1)		x	x	**x**		x	x
Cotoneaster racemiflora	F	+							**x**																

Sites		Djurdjura	Months							Aïn Kahla	Months							Seheb	Months						
Species	Part(s) eaten	% eating	F	M	A	M	J	J	A	% eating	F	M	A	M	J	J	A	% eating	F	M	A	M	J	J	A
Prunus prostrata	F	0.3 (2.4)				**x**																			
Erinacea anthyllis	Fl	0.8 (5.8)				**x**																			
Ononis aragonensis	L,F,S	0.7 (2.5)				x		**x**																	
Calycotome spinosa	L	0.2 (0.8)		**x**	x	x																			
Genista tricuspidata	L	+						**x**																	
Astragalus armatus	Fl,S	1 (4.4)				x	x	**x**	x																
Viburnum lantana	L									0.4 (1.6)			x	**x**				+			**x**				
Ilex aquifolium	F	0.1 (0.6)							**x**	0.1 (0.4)			**x**					+			**x**				
Rhamnus alaternus	F	+						**x**																	
Hedera helix	F	0.6 (4.1)					**x**			0.3 (1.3)			x	**x**											
Lonicera implexa	F	+							**x**																
Lonicera biflora	L	+			**x**																				
Daphne laureola	F									+						**x**									
Shrub undetermined	L,Fl,F	0.1 (0.4)			**x**	x			x																
Herbaceous layer																									
Ampelodesma mauritanicum	L,St	0.8 (3.3)	**x**	x	x	x	x																		
Avena macrostachya	S	+						x	**x**																
Arrhenaterum elatius	R	0.8 (5.4)						x	**x**									0.1 (0.7)						**x**	
Agropyron junceum	S									2.0 (9.2)						**x**	x								
Bromus rigidus	S,R									1.0 (3.7)					x	**x**		0.1 (0.7)							x
Bromus squarosus	S									0.5 (3.7)					**x**										
Bromus sterilis	S									1.2 (5.6)					x	**x**									
Dactylis glomerata	L,S,R	3.5 (13.1)	**x**	x	x	x				22.4 (76.0)	**x**	x	x	x	x	x	x	16 (79.4)	**x**	x	x	x			
Brisa maxima	S	+				**x**																			

Sites		Djurdjura	Months							Aïn Kahla	Months							Seheb	Months						
Species	Part(s) eaten	% eating	F	M	A	M	J	J	A	% eating	F	M	A	M	J	J	A	% eating	F	M	A	M	J	J	A
Dasypyrum breviarstatum	S									0.3 (1.7)					x		**x**								
Festuca geniculata	S									+							**x**								
Poa bulbosa	R									1 (4.4)				**x**		x	x	0.7 (5.1)						x	
Cruciata pedemontana	L																	1.2 (8.3)					**x**		
Melica cupanii	S									+						**x**									
Wheat	S									0.1 (0.4)							**x**								
Grasses undetermined	L,S,R	17.2 (47.5)	**x**	x	x	x	x	x	x	7.2 (29.5)				x	**x**	x	x	2.6 (10.1)			x			**x**	x
Luzula nodulosa	L	+			**x**																				
Asphodelus microcarpus	L,St,S	14 (50.9)		x	x	x	x	**x**	x																
Asphodeline lutea	S	0.3 (1.5)						**x**	x																
Tulipa silvestris	L,S,R	4.0 (11.2)			x		x	x	**x**	+							**x**								
Scilla sp	S,R	2.3 (10.9)				x	x		**x**																
Gagea foliosa	R																	0.1 (0.9)	**x**						
Ruscus aculeatus	L,F	1.7 (6.8)	x			x	**x**		x																
Ornithogallum umbellatum	R	0.3 (2.4)				**x**																			
Romulea sp.	L	+	**x**																						
Narcissus romieuxii	R																	0.1 (0.4)	**x**						
Narcissus tazeta	L	0.1 (0.5)	**x**	x																					
Cephalantera rubra	S	+							**x**																
Rumex acetosella	L	+	**x**																						
Rumex bucephalophorus	S	+				**x**																			
Cerastium gibraltaricum	L									+		x	x												
Cerastium glomeratum	L	0.2 (1.4)					**x**																		
Moerhingia trinervia	L	1.2 (6.8)			x	x	**x**																		

Sites		Djurdjura	Months							Aïn Kahla	Months							Seheb	Months						
Species	Part(s) eaten	% eating	F	M	A	M	J	J	A	% eating	F	M	A	M	J	J	A	% eating	F	M	A	M	J	J	A
Silene vulgaris	S									+						**x**									
Silene italica	Fl,S	0.3 (2.2)						**x**																	
Saponaria sicula	L	+							**x**																
Dianthus caryophillus	L,S	0.1 (0.7)			x			**x**	x																
Ficaria verna	L	+				**x**																			
Diplotaxis catholica	Fl	0.2 (1.2)				**x**																			
Iberis sempervirens	L	+			**x**																				
Brassica gravinea	L	+				**x**																			
Thlaspi perfoliatum	St									0.3 (1.2)			x	**x**				+			**x**				
Alysum sp.	R									+							**x**								
Cardamine hirsuta	L,R									+							**x**	+			x				
Arabis alpina caucasica	L,Fl	+			x	x																			
Arabis sp.	L									0.1 (0.3)	**x**	x													
Erysimum Bocconei	L	+			**x**																				
Umbilicus pendulinus	L	0.1 (0.4)		**x**						+							**x**								
Saxifraga globulifera	L	+				**x**																			
Saxifraga numidica	L	+		**x**																					
Saxifraga globulifera	L									0.1 (0.5)			**x**												
Sedum sp.	L									0.4 (2.5)			x		**x**		x								
Sedum multiceps	St	0.1 (0.4)							**x**																
Medicago suffruticosa	Fl,St,L,R									0.3 (0.6)				x	**x**	x	x	+				**x**			
Lotus corniculatus	L	+				**x**																			
Trifolium phleoides	Fl									2.1 (14.7)					**x**			0.5 (3.3)					**x**	
Trifolium campestre	Fl	1.0 (6.8)					**x**																		

Sites		Djurdjura	Months							Aïn Kahla	Months							Seheb	Months						
Species	Part(s) eaten	% eating	F	M	A	M	J	J	A	% eating	F	M	A	M	J	J	A	% eating	F	M	A	M	J	J	A
Trifolium hirtum	L	0.6 (3.6)				**x**		x																	
Trifolium sp.	L									0.6 (2.0)		x	x	**x**	x			0.4 (2.7)			**x**				
Onobrychis sp.	S									0.3 (2.3)						**x**									
Vicia sp.	S,L									0.6 (4.3)				x	**x**			0.2 (1.7)				**x**			
Geranium sp.	L									+				x											
Geranium malvaeflorum	L	+			**x**																				
Erodium sp.	R									0.2 (0.9)			**x**	x											
Erymgium campestre	L	+				**x**																			
Scandix australis	L	+				**x**																			
Heracleum spondilium	St									0.7 (3.6)			x	**x**	x										
Ferula communis	L	0.3 (1.2)	x	**x**		x																			
Bupleurum atlanticum	L	+				x																			
Balansea glaberrima	L,R	2.4 (4.9)	x	x	x	**x**	x	x																	
Carum montanum	R	0.7 (2.5)		x		x		**x**																	
Smyrnium olusatrum	R	+							x																
Smyrnium perfoliatum	L,R	0.7 (2.0)	x		**x**	x	x	x	x																
Bunium alpinum	R	+			x	x																			
Viola sp.	R	+						**x**																	
Armeria plantaginea	L	+	**x**																						
Labiaceae sp.	L	0.1 (0.5)	**x**																						
Phlomis bovei	L	+			**x**																				
Salvia argentea	Fl									0.1 (0.6)					**x**	x									
Teucrium flavum	L	+	**x**																						
Veronica hederefolia	St,L,F	+				**x**				0.4 (0.8)	x	x	x	**x**				0.3 (1.0)	x	x	**x**				

Sites		Djurdjura	Months							Aïn Kahla	Months							Seheb	Months						
Species	Part(s) eaten	% eating	F	M	A	M	J	J	A	% eating	F	M	A	M	J	J	A	% eating	F	M	A	M	J	J	A
Galium sp.	Fl,S ,St,L	+			**x**					1.4 (5.8)			x	**x**	x	x	x	0.7 (3.4)				x	**x**	x	
Galium perralderii	L	+				**x**																			
Asperula cynanchica	S	+							**x**																
Valeriana tuberosa	R	+			**x**																				
Knautia arvensis	Fl	0.3 (1.9)						**x**																	
Linaria heterophila	S,L									0.8 (1.8)				x	x	x	**x**								
Linaria sp	Fl									0.6 (4.3)					**x**			0.2 (1.7)					**x**		
Plantago sp.	R									+			**x**												
Bellis perrenis	St									+				**x**				+			**x**				
Bellis sylvestris	L,Fl	0.2 (1.2)				**x**																			
Phagnalon saxatile	L	0.3 (1.6)		**x**	x																				
Senecio gallicus	L	+				**x**																			
Senecio perralderianus	L	1.6 (6.8)	x	x	x	x	**x**																		
Asteraceae	Fl,L,S									0.1 (0.6)			x			x	**x**								
Atractylis sp	S									3.3 (17.5)						**x**	x								
Carlina atlantica	S									0.2 (1.2)					**x**	x	x								
Carduus sp.	Fl																	0.2 (0.7)						**x**	**x**
Carduus nutans macrocephalus	L,S	0.2 (0.5)				**x**		x																	
Cirsium syriacum	L,S	3.1 (18.7)	x			x		x	**x**																
Centaurea tougourensis	S	0.2 (1.1)						**x**	x																
Centaurea incana	L,R	+	x	x		x		x	x																
Centaurea sp.	S,L									0.2 (0.6)					**x**		x								
Catananche coerulea	S ,R ,L,St	0.5 (2.7)				x	**x**	x		0.8 (3.5)			x			**x**	x								
Hioseris radiata	L,Fl,R	2.8 (8.1)	x		x	x	**x**		x																

Sites		Djurdjura	Months							Aïn Kahla	Months							Seheb	Months						
Species	Part(s) eaten	% eating	F	M	A	M	J	J	A	% eating	F	M	A	M	J	J	A	% eating	F	M	A	M	J	J	A
Hypochoeris radicata	L,Fl	0.4 (2.8)					**x**																		
Hypochoeris laevigata	L,Fl	2.4 (11.0)	x			x	**x**	x	X																
Chrysanthemum sp.	St									+			x	**x**											
Mantisalca salmantica	L,S	+						**x**		0.1 (0.5)		x	**x**	x		x		+			x				
Carduncellus pinatus	S	+							**x**																
Scolymus grandiflorus	S	+							**x**																
Marrubium ayardii	R									+		x	x												
Onopordum acaulis	Fl,R									0.2 (0.6)		x		x	**x**	x	x								
Taraxacum obovatum	L	1.0 (4.1)				x	**x**																		
Lactuca intricata	R	+							**x**																
Jurinea humilis	L	0.1 (0.5)				**x**																			
Thymelea virgata	R,St																	0.9 (3.6)						**x**	x
Torilis elongata	L									0.3 (2.0)			x	**x**				+			**x**				
Herbaceous plant undetermined	R,L,S	0.2 (1.1)	**x**		**x**					1.6 (8.9)			x	x		x	**x**	1.3 (4.7)			x			x	**x**
Mushrooms		0.3 (1.5)			**x**	x				2.7 (6.8)		x	x	**x**	x	x	x	13.7 (48.3)	x	x	x	x	**x**	x	x
Animals																									
Bird	Egg									+				**x**											
Octolasium cyaneum	Ew									0.1 (0.6)		x		x	**x**			+		x	**x**				
Insects	Al,Ewg	0.3 (1.4)					**x**	x		0.8 (2.4)			x	x		x	**x**	6.4 (21.0)				x	x	**x**	x
Number of years of observations			1	1	2	1	1	1	1		1	1	2	2	1	3	3		1	1	2	2	1	2	2

B, bark; F, fruit; Fl, flowers; Ms, male strobiles; L, leaves; R, roots; S, seeds; St, stem; Sg, seedlings; Ac, acorns; Ew, earthworms; Ewg, adults and eggs of earwigs; Al, ant larvae. Mushrooms included two hypogeous fungi (*Geopora sumneriana* and *Tuber panniferum)* at Aïn Kahla and Seheb and undetermined above-ground fungi in Djurdjura. + : <0.05% of feeding time or rarely eaten food items recorded *ad libitum,* out of the scan sampling observations.